CASCADE
Catastrophic shifts in drylands:
How can we prevent ecosystem degradation?

CASCADE REPORT series

Report on indicators for critical thresholds

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CASCADE

Catastropic shifts in drylands

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Report on indicators for critical thresholds

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how CAn we prevent ecosystem DEgradation?

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Summary

One of the main goals of the European project CASCADE was to improve our understanding of the degradation of drylands which occupy 41% of the land area on Earth. Drylands are classical examples of ecosystems that may respond in abrupt, unexpected and often irreversible ways to gradual changes in external conditions, such as climate or land use changes [1–3]. Such abrupt responses have been referred to as *catastrophic shifts* in the ecological literature and can result in a reduction of the biological and, hence economic, potential of the land to support human populations, livestock and wild herbivores [3,4]. Because drylands support more than 38% of the human population, a fundamental understanding of their degradation process is crucial to define strategies to *predict* and *prevent* their degradation. To contribute to this goal, CASCADE combines empirical studies with the development of mathematical models, informed and improved by the empirical studies, to investigate how Mediterranean drylands cope with various levels of environmental stress.

A first deliverable (D6.1) presented the models developed in WP6 (Task 1 of the DOW), how the additional ecological mechanisms included in these models affected the response of the ecosystem to stress (Task 2 of the DOW), and focused specifically on identifying the conditions that favored the emergence of catastrophic shifts at the ecosystem scale.

Besides contributing to the general understanding of dryland dynamics and resilience, a crucial objective of the CASCADE project was to identify indicators of degradation in drylands. Previous theoretical studies have suggested the existence of generic indicators based on a phenomenon called 'critical slowing down' that occur in a wide class of systems when a critical threshold is approached. Additionally, indicators related to the spatial structure of the system have been proposed (e.g. patch size distribution, Flowlength). We use the term *generic early-warning signals* to refer to these two types of indicators. In this deliverable, we focus on these generic early-warning signals, which are promising indicators in the case where ecosystems exhibit possible catastrophic shifts, and we report on the progress that have been made regarding these indicators in CASCADE.

One of the main contributions of WP6 consisted in reviewing the generic early-warning signals currently available in the literature, testing their trends (in space and time) as an ecosystem is approaching a tipping point, and providing codes and information about these indicators to promote their broad use. We tested the limits of these indicators and identified conditions under which their signal can be blurred. In particular, our results highlight the importance of taking into account the characteristics of the main pressure at play (e.g. spatial component of grazing, intensity of rainfall events). In addition, new indicators were identified in the theoretical models developed in CASCADE, which can be added to the indicator toolbox and further evaluated and tested in future projects. Quantification of the indicators based on the spatial structure of the vegetation in dryland field data suggests that patch-size distributions can successfully reflect non-linear changes in dryland functioning and support the use of vegetation patterns as functional indicators in drylands.

Taken together, when quantified on increasingly available spatio-temporal dryland data sets, the indicator toolbox developed in WP6 could contribute to improve our ability to monitor degradation in drylands and thereby help set up effective strategies to prevent desertification before its onset (see CASCADE WP7 and WP8).

1. Introduction

Some ecosystems respond abruptly to small changes in environmental conditions, in which case ecosystems may shift to an undesired, and sometimes irreversible, state once a threshold of environmental condition, or *tipping point*, is passed [5]. A classic example of such *catastrophic shift* is the desertification of drylands (Fig. 1A; [3]). Despite the possible ecological and economic detrimental consequences of such ecosystem shifts, the conditions under which ecosystems exhibit abrupt, rather than gradual, responses to smooth changes in external conditions are not fully understood yet. Moreover, the prediction of upcoming ecosystem shifts before their occurrence would be extremely valuable to prevent them, but remains a challenge.

Drylands occupy 41% of the land area on Earth and support more than 38% of its human population [4]. Severe ecosystem degradation has already occurred in about 10–20% of drylands, and its consequences affect about 250 million people [3]. These values are likely to increase with climate change and current rates of human population growth [4,6]. Understanding and predicting how drylands respond to these ongoing environmental changes is extremely important for global sustainability [7], but challenging owing to the complex, dynamic interactions that exist among multiple drivers and ecosystem processes.

Within WP6, we developed a number of dryland vegetation models, starting from existing dryland models and sequentially including additional ecological mechanisms thought to be relevant for drylands' ability to cope with increasing pressures (Task 1 of the DOW). These mechanisms include modeling more realistic grazing pressures, modelling the effect of fire, taking the variability of the external pressure (rainfall) into account, incorporating different types of feedbacks such as erosion feedbacks known to be important for dryland functioning, taking different plant functional groups into account as a first step into taking more species characteristics into account (see CASCADE D6.1).

These dryland models were analyzed within WP6 to assess the importance of key ecological mechanisms for dryland dynamics and resilience (Task 2 of the DOW). Our model results highlight the importance of the role of the spatial component of external pressures (see §2.1 in CASCADE D6.1; [8]), demographic stochasticity (see §3.2.5 in CASCADE D6.1; [9]), rainfall intermittency and rate of environmental change (see §2.2.1, §2.2.2, §3.2.4 in CASCADE D6.1; [10–12]), the way species interact with each other (facilitation/competition) (see §2.2.1, §2.2.2, §3.2.1, §3.2.2, §3.2.3, §3.2.4, §3.2.5 in CASCADE D6.1; [9–15], and the relevance of different types of ecological feedbacks (see §2.2.2, §3.1 in CASCADE D6.1;[10,16]) for our understanding of the species composition and the dynamics of dryland ecosystems.

In particular our models can exhibit *alternative stable states*, and thereby possible shifts, between these alternative states, because of the presence of positive feedback loops between the different ecosystem components [5,17]. This means that for a range of conditions the ecosystem can be in one of two possible ecosystem states, for example one with high vegetation cover (Fig. 1A left picture) and another with low or no vegetation cover (Fig. 1A right picture). In such an ecosystem with two alternative stable states, referred to as a *bistable* system, small changes in environmental conditions lead to gradual ecosystem responses until a threshold, or *tipping point* (black dots in Fig. 1C), is reached at which the ecosystem shifts abruptly from one ecosystem state to a radically different one (orange and green arrows in Fig. 1C). These shifts are typically difficult to reverse once they have happened, if the recovery is possible at all. Such abrupt ecosystem responses are known as *catastrophic shifts*.

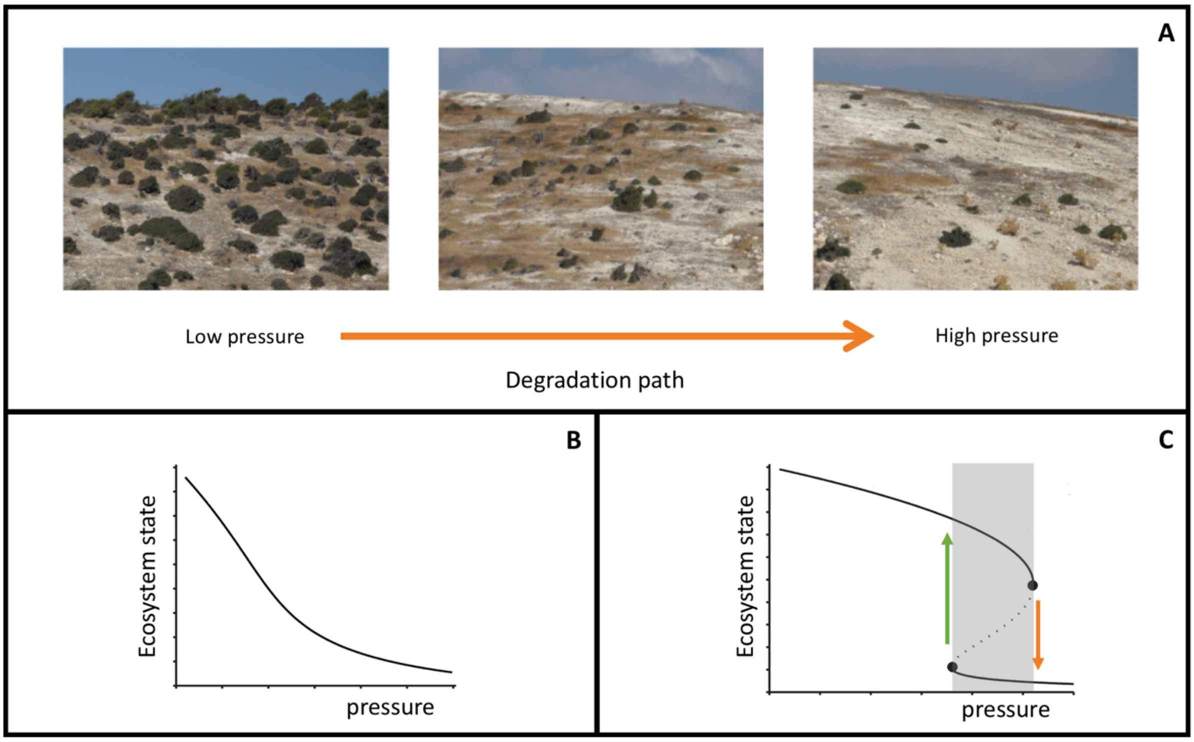

Figure 1: *Ecosystem response to gradual change in environmental stress. A: picture of a Mediterranean dryland ecosystem along a degradation gradient (from low stress in the left to higher stress on the right; pressure = grazing in this case). Photo credit: F.D. Schneider. Some ecosystems respond in a continuous, gradual and reversible way to increasing pressure (B), while others respond in an abrupt and unexpected manner (C). Solid lines represent the stable state of the ecosystem (e.g. vegetation cover in the case of Mediterranean drylands), black dots represent tipping points, and dashed lines represent the unstable state (the limit between the attraction basins of the stable states). In the case of the discontinuous ecosystem response of C, there is a range of pressure for which the ecosystem can be in either of two possible states (bistability area, in grey, between the tipping points) depending on the history of the system. In such a case, we are interested in identifying indicators of approaching tipping points (e.g. distinct behavior of some metric that would occur just before the collapse of the upper ecosystem state into the lower one, i.e. just before the ecosystem degrades along the orange arrow).*

If drylands can tip unexpectedly to a degraded state due to environmental changes, it is crucial to be able to detect such response in advance to prepare for it or avoid it. There are a number of indicators of ecosystem degradation available in the literature. For drylands, the probably most common one is the total amount of vegetation cover [18]. However, this indicator would typically fail in case a dryland is approaching a tipping point to desertification, because then the ecosystem abruptly shifts to a desert when it still has a relatively high vegetation cover (see e.g. [19,20] for discussions). In the last two decades, theoretical studies have suggested the existence of generic *early-warning signals* that may indicate if a tipping point is approached in a wide range of systems (see [21–23] for reviews). Additionally, in drylands, indicators related to the spatial structure of the vegetation cover have been proposed [24–26]. One of the core objectives of the European project CASCADE is to contribute to this body of research by identifying and testing indicators of degradation specifically for Mediterranean drylands (Tasks 3 and 4 of the DOW). Therefore, we used the models developed in CASCADE WP6 (see CASCADE D6.1) to identify signatures (i.e. changes in ecosystem characteristics) that occur especially as the ecosystem is approaching a tipping point to a degraded state, and defined those as possible indicators of degradations in drylands, i.e. (Fig. 1C; task 3 of the DOW). We then confronted these model-predicted indicators to data (Task 4 of the DOW). We present the results of these research projects in this second deliverable of WP6, D6.2.

2. Identification of the indicators

2.1. Generic early warning signals

Theoretical studies have suggested that a number of 'generic' indicators could be derived based on a phenomenon that appears to be universal prior to *bifurcations* (i.e. points at which the stability of a systems changes, such as a tipping point): *critical slowing down* [27]. Critical slowing down means that the time needed for a system to return back to equilibrium upon a small disturbance gets longer as the system approaches a bifurcation point (Fig. 2b-c). In other words, closer to a bifurcation, the system has a harder time recovering from perturbations, and the capacity of the system to absorb perturbations without shifting to a different state decreases.

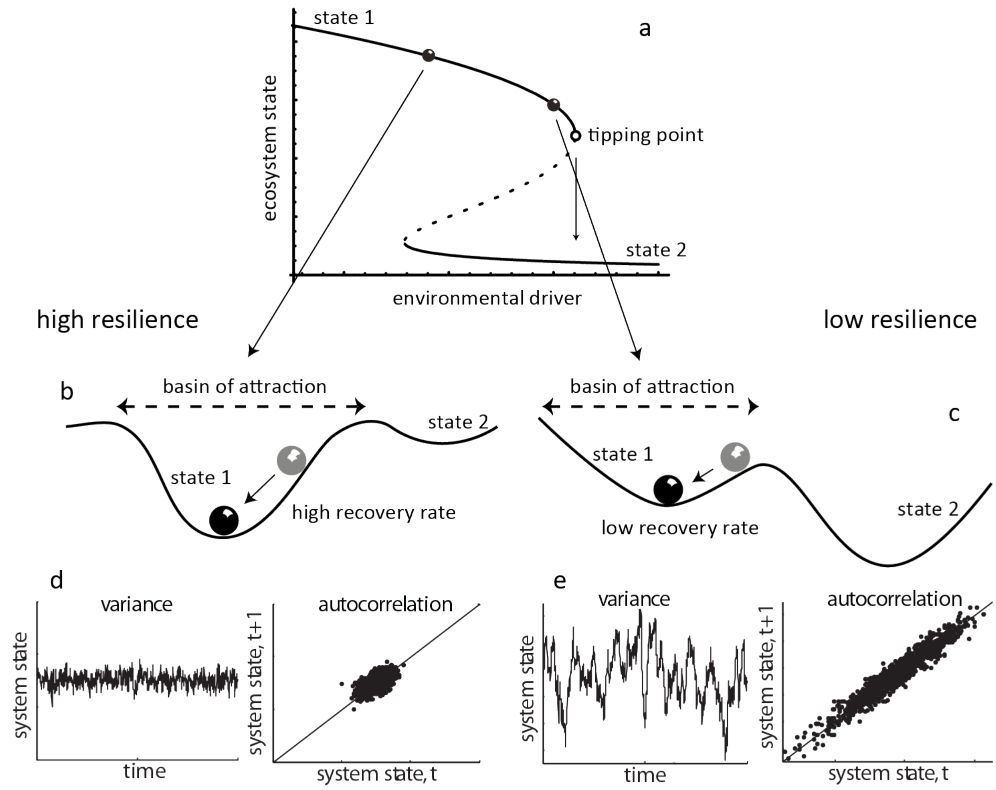

Figure 2: *Generic early warning signals. Far from the tipping point resilience is high (b): the ecosystem lies in a steep basin of attraction. Small disturbances are damped by high recovery rates back to equilibrium. Rate to recover from perturbations is high (b), the dynamics are characterized by low variance (d), and low correlation between subsequent states (d). Close to the tipping point resilience is low (c): the ecosystem lies in a less steep basin of attraction. Rate to recover from perturbations is low (c), the dynamics are characterized by high variance (e), and high correlation (e). Figure modified from [28].*

Critical slowing down has direct statistical signatures that have led to the definitions of *generic early-warning signals* of ecosystem degradation [21]. First, critical slowing down can be assessed by measuring the recovery rate of the system upon a disturbance (which should decrease as a system approaches a bifurcation point) [29] (Fig. 2b-c). Second, slowing down leads to an increase in variance prior to a tipping point: the state of the ecosystem should fluctuate more widely around its equilibrium [30] (Fig. 2d-e). Third, there is an increase in autocorrelation: the state of the ecosystem resembles more its previous state when it is close to a bifurcation point [31] (Fig. 2d-e).

In sum, theoretical models predict that recovery rate, variance and autocorrelation are statistical properties of the system dynamics that change in predictable ways prior to bifurcation points in general, and tipping points more specifically.

The generic early-warning signals have been developed and tested in a number of models (e.g. [32]). In harsh environments such as drylands, recruitment of woody plants often depends on nurse plants that ameliorate stressful conditions and facilitate the establishment of seedlings under their canopy. For example, C. Xu, S. Kéfi and colleagues [33] used an individual-based model and demonstrated that these facilitative interactions may cause a treeless and a woodland state to be alternative stable states on a landscape scale if nurse plant effects are strong and if the environment is harsh enough to make facilitation necessary for seedling survival (Fig. 3A). A corollary is that under such conditions, environmental change can bring drylands to tipping points for woody plant encroachment (path 4-3-1 in Fig. 3A) or woodland collapse (path 1-2-4 in Fig. 3A). We showed that the proximity of tipping points can be announced by the generic early-warning indicators, i.e. by slowness of recovery of woody vegetation cover from small perturbations (because of critical slowing down; Fig. 3B, C) as well as by elevated temporal and spatial auto-correlation and variance (Fig. 3D-G).

The genericity of early warning signals

Most studies on the generic early-warning signals had initially focused on models exhibiting tipping points and catastrophic shifts, and it was unclear how these indicators behaved in systems approaching other types of bifurcations. In particular, it was unclear whether the early-warning signals were specific to catastrophic shifts or whether they could also occur in cases of abrupt but reversible ecosystem responses. In the context of CASCADE WP6, we tested the behavior of the generic early-warning signals as a model system approached different types of bifurcations [34].
We found that all indicators showed consistent patterns for a variety of bifurcations. In particular, we found that the generic early-warning signals were not specific to catastrophic bifurcations but also preceded non-catastrophic transitions [34]. The generic early-warning signals can generally be detected in situations where a system is slowing down, i.e. becoming increasingly sensitive to external perturbations, independently of whether the impeding change is catastrophic or not.

These results highlight that slowing down and its statistical signatures can generally be used as indicators of degradation, also in systems where we have no reason to expect catastrophic transitions. Our results also imply that indicators specific to catastrophic shifts are still lacking.

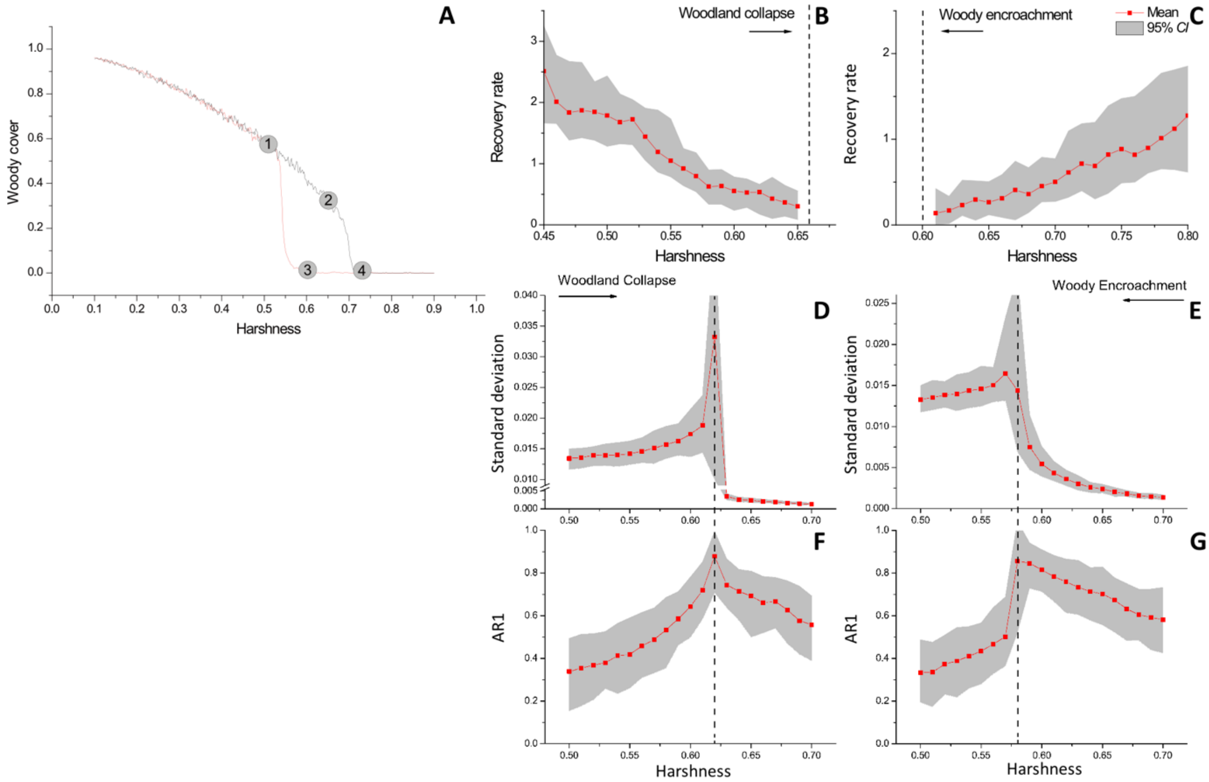

Figure 3: *A. Change in woody cover as a function of environmental harshness. As harshness increases, the woodland collapses catastrophically into a treeless state (path 1-2-4). After a collapse, a decrease in environmental harshness can lead to an abrupt recovery of the woody vegetation following the path 4-3-1. The ecosystem therefore exhibits two tipping points located around point 2 (woodland collapse tipping point) and point 3 (woody encroachment tipping point). B-C: The recovery rate of the ecosystem upon small perturbations slows down towards both tipping points (dashed lines). D-G: Temporal indicators of critical slowing down. Variance (standard deviation, D-E) and temporal correlation (lag-1 autoregressive coefficient, AR1, F-G) in simulated time series rise towards tipping points (dashed lines) for a shift from high to low woody cover (woodland collapse) as well as for a shift from low to high woody cover (woody encroachment). Figure modified from [33].*

2.2. Spatial generic early warning signals

Indicators specifically based on spatial information

Studies have shown that slowing down in space takes place in an analogous way as slowing down in time [35,36]. Spatial variance and spatial correlation between near-neighbors are expected to rise as a system is approaching a bifurcation point. However, in models that show a strong spatial structure, like drylands, it has been shown that most of the generic early warning signals can fail [32]. In such cases, indicators specific to those systems need to be developed.
In drylands, vegetation is characterized by spatial patterns formed by the isolated vegetation patches interspersed with bare soil (Fig. 1A). In addition to the spatial generic early warning signals, studies have suggested that changes in the spatial vegetation patterns themselves could be indicative of environmental deterioration in semi-arid ecosystems [24,26]. In

particular, the shape of the vegetation patches [1,37] and the distributions of vegetation patch sizes could indicate that an ecosystem is degrading [25,26].

In the context of WP6, we reviewed these spatial indicators of ecosystem degradation suggested by the theoretical literature [23] (early-warning signals and patch-based indicators), and we developed a methodological framework for the practical quantification and the interpretation of these indicators on real data (Fig. 4).

We developed a statistical toolbox (the *earlywarnings package*) in the free programming R environment whose code is freely available online as well as a webpage aiming at describing and explaining the various indicators (in time and space) and their theoretical foundation, giving some concrete examples of case studies and references from the literature (see §5 of this deliverable for more information).

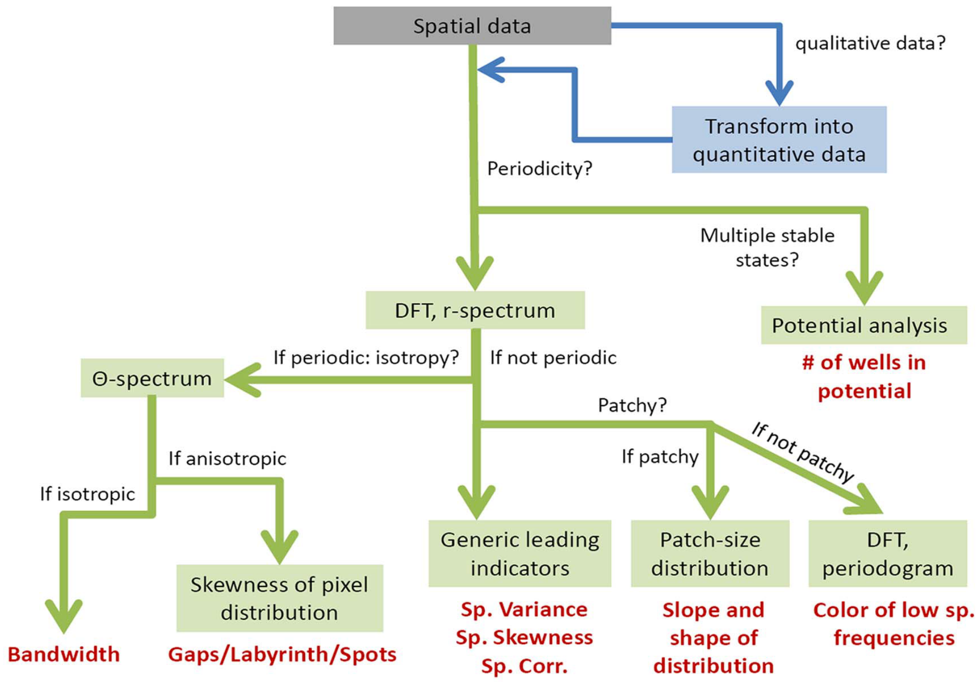

Figure 4: *Flow chart of the analyses to perform on a spatial data set to quantify indicators of degradation along stress gradients. Figure from [23].*

2.3. Refining the understanding and use of indicators

Patch-based indicators and spatial stressors

The theoretical foundations of early warning signs of catastrophic shifts had so far assumed that pressures on ecosystems distribute homogeneously in space. While this may be valid for some pressures, it is most certainly not true for others such as livestock grazing, which is not only a major human supply factor, but also a primary trigger of desertification. In CASCADE

WP6, F.D. Schneider and S. Kéfi developed a dryland vegetation model including grazing and its spatial component (see CASCADE D6.1; [8]), and we investigated the behaviour of the spatial indicators of degradation in this model.

Our model analysis shows that spatially-explicit grazing disrupted patch growth and put even apparently 'healthy' drylands under high risk of catastrophic shifts (Fig. 5). Our study highlights that the spatial indicators of degradation can fail in ecosystems where the pressure is spatially heterogeneous, such as grazed drylands. Our results may very well generalize to other ecosystems exhibiting self-organized spatial patterns where a spatially-explicit pressure disrupts pattern formation.

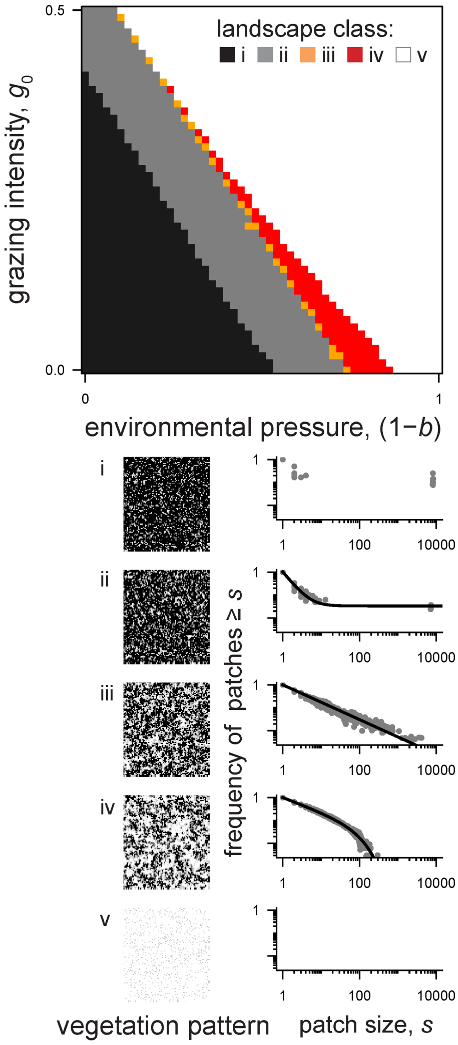

Figure 5: *Landscapes classified based on the cumulative patch size distribution of the vegetation (i: full cover; ii: up-bent power law with spanning clusters; iii: pure power-law; iv: down-bent power law; v: desert) along gradients of environmental and grazing pressures. Note that at high grazing pressure, a vegetation collapse was not preceded by down-bent power laws. Figure adapted from [8].*

Periodic patches and patch adaptation in response to environmental changes

In WP6, Koen Siteur, Max Rietkerk and colleagues [38] studied a simplified vegetation reaction-diffusion-advection model producing periodic vegetation patterns. Model studies revealed that patterned ecosystems may respond in a non-linear way to environmental changes, meaning that gradual changes can lead to sudden desertification. In Siteur et al. [38] we studied this response through a novel stability analysis of patterned vegetation states. We found that, besides direct critical transitions through decreased rainfall, patterned vegetation states may also adapt, depending on the rate of environmental change and the amount of noise. Rapid environmental change and lack of noise resulted in a drastic critical transition (top right panel), while patterns could adapt in the case of slow environmental change (top left panel). In the model, the vegetation patterns adapted to environmental change in two ways: 1) by adapting biomass while the wave number of the periodic patches remained the same and 2) by adapting wave numbers. We were able to construct so-called 'Busse balloons', showing the surface in parameter planes for which stable patterned vegetation states can be found (grey area). These findings shed a more nuanced light on the earlier suggestions that regular patterns in those systems would indicate bistability and proximity to catastrophic shifts [24,37]. Indeed, these model results suggest that ecosystems may adapt and catastrophic shifts may be avoided, if environmental changes are sufficiently slow.

Including rainfall intensity

How annual and seasonal rainfall volumes in arid and semiarid regions will change in the coming decades is subject to much uncertainty, according to global climate model projections. In contrast, projections of changes in rainfall intensity show strong trends. Rainfall intensity has an important impact on spatial infiltration patterns of water in patchy arid ecosystems [39,40], and it is unknown if and exactly how the projected changes in rainfall intensity are going to affect the productivity and functioning of patterned semiarid ecosystems.

In WP6, K. Siteur, M.G. Rietkerk and colleagues [41] performed a model analysis to address that question and concluded that projected increases in rainfall intensity could induce and enhance alternative stability of semiarid ecosystems. We also found that under certain conditions both an increase and a decrease in mean rainfall intensity could push the system over a critical threshold, resulting in a regime shift to a bare desert state. This finding was attributed to the fact that water can be lost from the system in two ways. During high intensity rain events, a fraction of the water flows through the vegetation bands and is lost as runoff, while during low intensity events a large portion of the water infiltrates in the bare interbands, where it is less available to plants and can eventually be lost due to soil evaporation and percolation.

> This study suggests that considering rainfall intensity as a variable may help in assessing the proximity to regime shifts in patterned semiarid ecosystems, and that monitoring losses of resources through runoff and bare soil infiltration could be used to determine ecosystem resilience.

2.4. Developing new, additional indicators

In addition to the early-warning signals and the patch-based indicators, new indicators were also suggested in CASCADE, which are hereafter presented (see Table 1 for an overview of all these indicators).

Hydrologically-based indicators: *Flowlength* (connectivity-based indicators)

Vegetation cover and pattern, and therefore the bare-soil connectivity, largely determine runoff and thereby the potential of the ecosystem to conserve (or leak) resources such as water, soil and nutrients. An indicator of degradation based on bare-soil connectivity was developed, referred to as *Flowlength* [42]. Flowlength measures the connectivity of bare-soil areas in a given landscape (by calculating the average of the runoff pathway lengths from all the cells in the system), and thereby estimates the potential of the landscape to lose resources. Flowlength assumes that bare-soil areas behave as sources of runoff and sediments that are trapped by downslope vegetated areas, which behave as sinks of resources.

In the context of WP6, A.G. Mayor and colleagues [16] modeled the effect of landscape resource loss (estimated with Flowlength) on plant establishment in a dryland vegetation model. Our model analysis showed a non-linear inverse relationship between bare soil connectivity (here Flowlength) and vegetation cover. This means that if bare-soil connectivity increases above certain values (for example because of cover loss), a disproportional loss of resources would take place, greatly limiting plant establishment. This results in a positive feedback which accelerates the shift of the ecosystem into a degraded state (CASCADE D6.1; [16]). In other words, considering the effect of bare-soil connectivity on vegetation recruitment increases the probability of catastrophic shifts in dryland.
Our results further suggest a higher sensitivity of the bare-soil connectivity index (Flowlength index) to changes in the spatial organization of the vegetation during the transition to a degraded state, in comparison with bare-soil (or vegetation) cover, which shows a rather linear evolution during this transition. This means that bare-soil connectivity could be a better indicator of degradation that bare soil.

Our study suggests that changes in vegetation pattern and associated hydrological connectivity may be more informative early-warning indicators of dryland degradation than changes in vegetation cover. An acceleration of bare-soil connectivity observed in spatially-explicit time-series data may therefore provide an early warning of imminent shift.

Network-based indicators

In WP6, Max Rietkerk and collaborators investigated a vegetation model that exhibits a catastrophic shift to desertification, and translating spatio-temporal data (i.e. a simulated field of vegetation biomass) into a network of interactions [43]. A network is defined by two sets of objects, the so-called *nodes*, and the set of their mutual connections, namely their *links*.
The nodes were defined as the biomass grid cells of the discretized model. To define the links between the nodes, the zero-lag temporal correlations between the biomass time series at the different nodes were considered. More precisely, two nodes were linked, if the temporal

cross-correlation of the time series of two nodes were statistically different. The most basic characteristic of a network is called its degree distribution, for which the degree of a node is defined as the number of links of the node. We followed the changes in network properties, here the mean and the variance of the node degrees, changed along the transition to desertification.
We found that the average and variance degree showed a markedly increase when decreasing rainfall in the model, before it collapsed at a certain rainfall rate. Our study suggests that basic network characteristics could offer novel indicators for identifying an upcoming desertification in semi-arid ecosystems [43]. For instance,

Comparing the performance of these network-based indicators with the generic early-warning signals based on variance and autocorrelation, we found that network-based indicators were more sensitive to the presence of the transition point. The network based indicators hence offer a promising alternative to detect ecosystem degradation.

Indicator name	Description	Advantages	Drawbacks	References
Cover	Percentage of the ground covered by vegetation	Easy to understand, easy to measure	Fails in the case of ecosystem shift	[18–20]
Temporal generic indicators	Temporal variance, auto-correlation at lag 1 and temporal skewness calculated on time series of a variable of the ecosystem state (e.g. cover, abundance of a key species…)	Works independent of the type of changes expected in the ecosystem (i.e. both with continuous degradation and catastrophic shifts)	Requires to use more advanced statistical tools (but tools freely available); Requires detailed time series of the variable	[21,22]
Spatial generic indicators	Spatial variance, near-neighbour correlation and spatial skewness calculated on spatial data (e.g. aerial images on which vegetation abundance or presence/absence can be estimated in space)	Works independent of the type of changes expected in the ecosystem; Only a few spatial snapshots in time are required to get an idea of the trend that an ecosystem follows through time	Requires to use more advanced statistical tools (but tools freely available) Requires spatial data or maps with sufficient resolution	[21,23]
Patch-based indicators	Metrics quantifying the shapes, sizes, distribution of patch sizes present in the landscape and power law range (PLR, i.e. the proportion of the distribution that fits a power law)	More powerful than generic indicators for patchy landscapes (i.e. landscapes with a strong spatial structure); Works independent of the type of changes expected in the ecosystem	Only works on patchy landscapes; Requires to use more advanced statistical tools (but tools freely available) Requires spatial data or maps with sufficient resolution	[23,25,26,32]
Flowlength	Metric quantifying the connectivity of bare-soil areas in the landscape, which is a proxy for how much resource can be lost from the system.	More powerful than cover for patchy landscapes; Works independent of the type of changes expected in the ecosystem	Only works on patchy landscapes; Requires to use more advanced statistical tools	[16,42]
Network-based indicators	Metrics calculated on spatial data after transformation them into a network of interaction. In such network the mean and variance of the node degree are followed.	More powerful than generic indicators	Requires to use more advanced statistical tools	[43]

Table 1: *Table summarizing the different indicators studied in WP6.*

3. The validation of the indicators

The development of early warning signals to detect the onset of regime shifts in marine and terrestrial ecosystems has received increasing attention during the last decade. The theoretical interest for these indicators has created a novel and promising framework for studying tipping points in ecological systems. The challenge, however, is whether these indicators can be applied in reality.

To evaluate the indicators, and more precisely the patch-based indicators, as indicators of dryland degradation, we used a data set from another European project, BIOCOM, coordinated by Fernando Maestre (Madrid, Spain) [44]. This work is part of the Ph.D. thesis of Miguel Berdugo, co-supervised by Sonia Kéfi, Fernando Maestre and Santiago Soliveres. The database contains vegetation and soil data of 224 drylands from all around the world. For each site, the dataset contains the estimated plant cover, the frequency of positive plant-plant interactions, 16 soil variables (related to the carbon, nitrogen and plosphorous cycles) hereafter called 'functions', and the aridity index (AI, precipitation/potential evapotranspiration).
From these sites, we retained for this study those from which we could gather Google Earth™ (https://earth.google.com/) or VirtualEarth™ (http://www.bing.com/maps) images good enough for visually identifying vegetation patches. The resulting 115 sites used for the analyses are located in 13 countries and differ widely in their abiotic (elevation, temperature and precipitation) and biotic (vegetation type, cover and number of species) features.
We used the combination of remote sensing and field data to evaluate the links between vegetation cover, patch-size distribution and multifunctionality (the ability of ecosystem to provide several soil fertility related services at the same time; it was measured as the average Zscore of the 16 soil variables; see [44] for a description of the approach).

We found that the observed vegetation patch-size distributions always fitted heavy-tailed distributions with varying levels of curvature (such as in Fig. 5). Distributions showing strong curvatures have a relatively low proportion of patch sizes that fit a power law (i.e. a low Power Law Range, hereafter referred to as PLR). These curvatures are caused by the lack of the largest and/or of the smallest vegetation patches compared to what would be expected in a pure power law: *PL-like sites* whose patch size distribution fits best a power law, and ii) and *non PL-like sites* which had more curved distributions.

Moreover, we found a bimodal distribution of multifunctionality values in our field sites, which suggests contrasting multifunctionality states in global drylands. This can be interpreted as the existence of two alternative states in multifunctionality in global drylands. More specifically, mapping the number and value of estimated alternative states along the aridity gradient studied reveals a range of aridity values (between 0.2 and 0.4, meaning that 1-AI is between 0.6 and 0.8) for which two multifunctionality levels coexist across our sites (Figure 7). The type of patch-size distribution was significantly associated with the two multifunctionality states observed (PL-like sites in the upper branch and non-PL-like sites in the bottom branch).

Changes in patch-size distributions indicate a spatial reorganization of the existing cover, which is related to processes influencing the functioning of drylands, such as soil erosion.

Modifications in spatial patterns can also reflect important variations in the structure of plant communities unrelated to changes in cover.

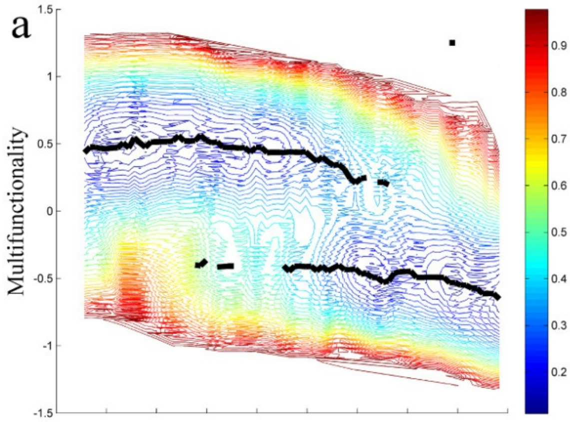

Figure 7: *Relationship between aridity (x-axis) and multifunctionality (y-axis). Variation of the 'stable' states (i.e. local minima of the stability landscape (black line) along the aridity gradient studied for multifunctionality. AI = aridity index (annual precipitation / annual evapotranspiration). Contour lines represent the estimated potential energy from which the 'stable' states are derived as local minima, i.e. blue color represent more stable states and red color represent less stable states. Figure from [45].*

Our results show that while plant cover is the best linear predictor of multifunctionality in global drylands, patch-size distributions are better reflecting non-linear changes in this variable. Our findings support the use of vegetation patterns as functional indicators in drylands, and pave the way for developing effective strategies to monitor desertification processes.

4. Conclusion

Because of the possibly dramatic consequences of dryland degradation for the livelihood of about 250 million people living in drylands, it is of crucial importance to understand why and how these ecosystems respond in abrupt, unexpected and often irreversible way to gradual external changes as well as to identify indicators of such response. These were key research questions addressed within CASCADE WP6.

In this second deliverable of WP6, we reviewed the advances made in WP6 regarding the knowledge and evaluation of currently available indicators in theoretical models of degradation for dryland ecosystems (see Table 1 for an overview of those indicators).

More precisely, within WP6:
- we reviewed the generic early-warning signals available in the literature – those particularly available to drylands (§2.1; [46]),
- we evaluated and discussed the applicability and limits of these indicators (§2.1, 2.2., 2.3; [8,33,34,41]),
- we proposed new indicators (§2.4; [16,43,47]),
- we tested the patch-based indicators on field data (§3; [45]),
- we developed and provided codes and information for transmission of these indicators (webpage, code R; see upcoming §5).

We hereafter go through the main results of this deliverable, their implications for management and provide some directions for future investigations.

4.1. Main results

A number of indicators of ecosystem degradation are currently available in the literature (see Table 1 for those studied in WP6). So-called generic early-warning signals are simple metrics (return rate after a perturbation, variance, correlation) based on the phenomenon of critical slowing down, which occurs when a system approaches a bifurcation point, i.e. a point at which the system stability is going to change drastically. These indicators can be quantified on both temporal and spatial data. In the case of spatially-structured ecosystems, such as drylands, these generic indicators have been shown to be very likely to fail [32], and additional indicators, based on the ecosystem spatial structure have been suggested: in particular the shape of the vegetation patches and the shape of the patch size distribution.

In WP6, we reviewed these indicators, and proposed a work flow of how to quantify them on real data (§2.2; [46]). The code to apply these indicators on ecological data (e.g. aerial images of the landscapes) has also been made available (§5).

These indicators were tested in a number of more particular cases, and we identified situations in which they are expected to fail. In particular, by comparing their behavior along different types of transitions, we showed that they are not specific to catastrophic shifts, but also occur along non-catastrophic transitions (§2.1; [34]): they are therefore indicators of ecosystem degradation because their detection points to the fact that the ecosystem is having a harder time recovering from perturbations, but they do not indicate what type of transition the system is approaching. A model study taking the spatial component of grazing into account (§2.3) showed that this mechanism, by affecting vegetation patch growth, affected ecosystem resilience (by increasing the probability of catastrophic shifts at high grazing pressures) and the efficiency of patch-based indicators at announcing upcoming ecosystem degradation [8]. This grazing model analysis warns about the blind use of the patch-based degradation indicator without knowing the characteristics of the stressor and their interactions with the intrinsic mechanisms of the ecosystem. Another model study focusing on rainfall intensity (§2.3), one of the major changes expected in dryland climate in the coming decades, suggested that explicitly considering rainfall intensity may help in assessing the proximity to regime shifts in patterned semiarid ecosystems, and that monitoring losses of resources through runoff and bare soil infiltration could be used to determine ecosystem resilience [41].

A number of studies performed in WP6 additionally proposed new indicators or approaches. Using a dryland vegetation model, including erosion feedbacks, Mayor et al. [16] suggested that changes in bare-soil connectivity along a degradation gradient (resulting from changes in both plant cover and spatial patterns) may be more informative than changes in plant cover as early-warning indicators of dryland degradation (§2.4). This is in agreement with recent empirical evidence [48]. Moreover, we found that basic network characteristics could offer novel indicators for identifying an upcoming desertification in semi-arid ecosystems and that the performance of these network-based indicators could be superior to these of the generic early-warning signals based on variance and autocorrelation (§2.4; [43]).

Finally, the last task of WP6 was to evaluate these indicators on real data in an attempt to validate their use and efficiency. To do this, we used a large-scale data set from another European project, BIOCOM, in which we could quantify patch-based indicators on 115 dryland sites located world-wide and compare them to field-based measurements reflecting ecosystem functioning (summarized in a metric called *multifunctionality*). We found that abrupt changes in multifunctionality along an aridity gradient could be reflected by the patch-size distribution of vegetation. By providing the first link between plant spatial patterns and multifunctionality in global drylands, our study provides strong empirical and mechanistic support to the use of these patterns as indicators of discontinuous changes in ecosystem functioning.

4.2. Implications for management

The results of CASCADE WP6 have a number of practical implications in terms of predicting dryland degradation:

- Our results provide support for the use of indicators based on the spatial structure of the vegetation cover (patch-size distribution, Flowlength) to assess the ecosystem degradation level (§3).
- Our results nonetheless warn about the need for well identifying the main stressors at play in the ecosystem considered (see rainfall and grazing in §2.3) since they can affect the type of indicator to follow and their reliability.
- Our studies have put forward a number of new indicators (Flowlength and network-based indicators; see Table 1) that need further testing and validation in future studies.

Jointly, all those indicators, when simultaneously evaluated and if they all converge in their trends, can help identifying the critical point at which measures should be adopted to prevent drastic changes in ecological conditions before they happen. These spatial indicators can be evaluated on spatio-temporal ecosystem data that are becoming increasingly available through e.g. aerial images.

More globally, our results suggest that ecosystems with aridity indices between 0.2 and 0.4 are especially sensitive to further disturbances [45]. In areas where aridity is expected to reach such values in the future [49] or where grazing is rising due to a higher demand in livestock products, such increased pressures could force the sites in this sensitive climatic envelope into a low multifunctionality state (i.e. degradation). A key result of our study is that these abrupt changes in multifunctionality can be reflected by the patch-size distribution of vegetation, which is related to critical changes in the way dryland ecosystems are organized.

4.3. Outlook

Our results also pave the way for more systematically testing these indicators, in various dryland sites (worldwide) and under various drivers, since our model analyses suggest that the nature of the driver and its characteristics can affect the efficiency and the reliability of the indicators. Steps in that direction have already being initiated in CASCADE WP6 (e.g. analyses of spatial images from CASCADE field site by Utrecht University Ph.D. student Myrna de Hoop).

Simultaneously, the statistical tools needed to evaluate these indicators needs to be developed, tested and made available so that they can be widely applied. As already mentioned, tools and information about them have already been made available by CASCADE WP6 and these tools will keep being updated (see §5 for more information).

A key element currently lacking from the validation of the indicators is a quantitative measure of the pressure at play. In the work of Berdugo and colleagues (§3 ; [45]), the indicators of ecosystem degradation have been clearly correlated with metrics reflecting ecosystem functioning (so-called multifunctionality), but no measure or information about the pressures at play in the different field sites available were available. Again, a step in that direction will be taken by the upcoming study from Myrna de Hoop since dung counts have been measured in the field in that case and can constitute a proxy for the level of grazing pressure. Moreover, quantifying anthropogenic pressures is an explicit goal of a newly funded European project on desertification, BIODESERT (coordinated by Fernando Maestre).

5. Sharing and communicating WP6 results

Accompanying our review of the spatial indicators of degradation currently available in the literature [23], we developed a statistical toolbox ("earlywarnings package") in the free programming R environment whose code is freely available online:
https://github.com/earlywarningtoolbox/spatial_warnings
This toolbox allows quantifying all spatial indicators reviewed in [23] on spatial data sets. The toolbox is constantly being updated. Alexandre Génin (Ph.D. student in Montpellier with Sonia Kéfi) is working on the next version of the code with Sonia Kéfi. This new version will be made available in 2017.

With our collaborator Vasilis Dakos, we also set up a webpage aiming at describing and explaining the various indicators (in time and space) and their theoretical foundation, giving some concrete examples of case studies and references from the literature (Fig. 8):
http://www.early-warning-signals.org/
This webpage will also keep being updated with the latest development regarding spatial indicators.

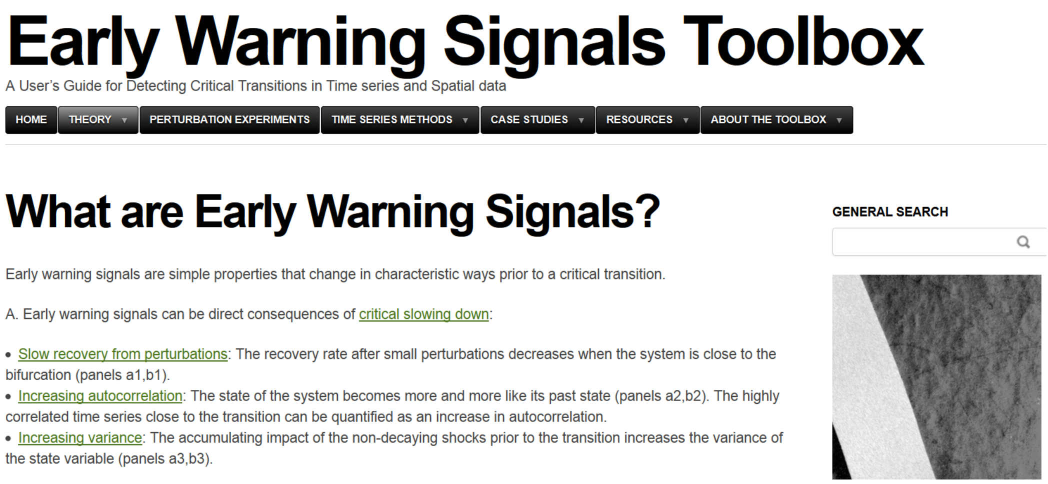

Figure 8: *Print screen of the early warning signal webpage.*

Appendix: List of products from WP6 D6.2

Kéfi, S., V. Dakos, M. Scheffer, E.H. van Nes, and **M. Rietkerk**. 2013. Early warning signals also precede non-catastrophic transitions. Oikos 122: 641-648.

Mayor A.G., Kéfi S., Bautista S., Rodríguez F., Cartení F., **Rietkerk M.**, 2013. Feedbacks between vegetation pattern and resource loss dramatically decrease ecosystem resilience and restoration potential in a simple dryland model. Landscape Ecology 28:931-942.

Kéfi, S., V. Guttal, W.A. Brock, S.R. Carpenter, A.M. Ellison, V. Livina, D.A. Seekell, M. Scheffer, E.H. van Nes, V. Dakos. 2014. Early Warning signals of ecological transitions: Methods for spatial patterns. PLoS ONE 9(3): 2097.

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Petchey, O.L., M. Pontarp, T.M. Massie, **S. Kéfi**, A. Ozgul, M. Weilenmann, G.M. Palamara, F. Altermatt, B. Matthews, J.M. Levine, D.Z. Childs, B.J. McGill, M.E. Schaepman, B. Schmid, P. Spaak, A.P. Beckerman, F. Pennekamp, I.S. Pearse. 2015. The ecological forecast horizon, and examples of its uses and determinants. Ecology Letters. 18(7): 587-611.

Xu, C., E.H. Van Nes, M. Holmgren, **S. Kéfi**, and M. Scheffer. 2015. Local facilitation may cause tipping points on a landscape level preceded by early warning indicators. American Naturalist. 186(4): E81-E90.

Schneider, F.D., S. Kéfi. 2016. Spatially heterogeneous pressure raises risk of catastrophic shifts. Theoretical Ecology. 9(2): 207-217.

Berdugo M., **Kéfi S.**, Soliveres S., Maestre F.T. 2017. Plant spatial patterns identify alternative ecosystem multifunctionality states in global drylands. Nature in Ecology and Evolution. In press.

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